

Modeling Wetland Blackbird Populations as a Function of Waterfowl Abundance in the Prairie Pothole Region of the United States and Canada

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Blackbirds share wetland habitat with many waterfowl species in Bird Conservation Region 11 (BCR 11), the prairie potholes. Because of similar habitat preferences, there may be associations between blackbird populations and populations of one or more species of waterfowl in BCR11. This study models populations of red-winged blackbirds and yellow-headed blackbirds as a function of multiple waterfowl species using data from the North American Breeding Bird Survey within BCR11. For each blackbird species, we created a global model with blackbird abundance modeled as a function of 11 waterfowl species; nuisance effects (year, route, and observer) also were included in the model. Hierarchical Poisson regression models were fit using Markov chain Monte Carlo methods in WinBUGS 1.4.1. Waterfowl abundances were weakly associated with blackbird numbers, and no single waterfowl species showed a strong correlation with any blackbird species. These findings suggest waterfowl abundance from a single species is not likely a good bioindicator of blackbird abundance; however, a global model provided good fit for predicting red-winged blackbird abundance. Increased model complexity may be required for accurate predictions of blackbird abundance; the amount of data required to construct appropriate models may limit this approach for predicting blackbird abundance in the prairie potholes.

Keywords blackbirds, Bayesian, hierarchical, waterfowl, prairie pothole region, abundance

Introduction

Red-winged blackbirds (*Agelaius phoeniceus*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) are two abundant blackbird species that inhabit marshes and fields in Bird Conservation Region 11 (BCR11), the Prairie Potholes (Twedt and Crawford 1995, Yasukawa and Searcy 1995). Stewart and Kantrud (1972) noted these two blackbird (Icteridae) species accounted for nearly 9% of the avian abundance in North Dakota. While blackbirds are declining in some parts of their range (e.g., Blackwell and Dolbeer

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2001), their populations in BCR11 have been stationary or have increased slightly in the past 20 years (Sauer and others 2005).

Populations of blackbird species depredate millions of dollars in agricultural crops across the United States every year. Damage that blackbirds cause is mostly due to their flock feeding and communal roosting behaviors combined with their large numbers (Weatherhead and Bider 1979). Blackbirds predate several economically significant crops including rice, sunflower, and corn (Hothem and others 1988, Labisky and Brugger 1989, Dolbeer 1990). In BCR11, sunflower damage is particularly pronounced with many growers reporting damages exceeding 10% (Lamey and others 1993). Overall sunflower damage is much lower with statewide estimates in North Dakota and South Dakota averaging 2.2% (Linz and others 2000). Total damage estimates of sunflower damage in the northern Great Plains range from \$5.1 million to \$7.9 million (Hothem and others 1988). Recent models by Peer and others (2003) estimate damage closer to \$5.4 million; percents of the total damage caused by each species are red-winged blackbirds (52%) and yellow-headed blackbirds (20%). Because of their importance to agroecconomics, estimating relative annual population fluctuations of blackbirds can provide valuable information to wildlife managers and sunflower growers.

Blackbirds in BCR11 share wetland habitat with a variety of other wetland-dwelling waterbirds. Because waterbirds inhabiting BCR11 appear to have similar habitat requirements to blackbirds, it is possible that relationships exist between breeding blackbird numbers and populations of other birds that use similar habitat. Species of waterfowl that nest in the BCR11, such as the American wigeon (*Anas americana*) (Mowbray 1999), gadwall (*Anas strepera*) (LeSchack and others 1997), green-winged teal (*Anas crecca*) (Johnson 1995), northern pintail (*Anas acuta*) (Austin and Miller 1995), blue-winged teal (*Anas discors*) (Rohwer and others 2002), and the northern shoveler (*Anas clypeata*) (Dubowy 1996), nest habitat including native prairie, old cropland, hayfields, and field borders. Only a few species of waterfowl, such as the canvasback (*Aythya valisineria*) (Mowbray 2002) and the redhead (*Aythya americana*) (Woodin and Michot 2002), nest in dense, emergent vegetation (Stewart 1975).

This study evaluates using populations of different waterfowl species as bioindicators for populations of red-winged blackbirds and yellow-headed blackbirds. This is accomplished by modeling red-winged blackbird and yellow-headed blackbird abundance as a function of the abundance of 11 different waterfowl species. Elucidating relationships between waterfowl and blackbird abundance will show how species from each taxa relate to one another and vary over time. The ability to use waterfowl species as a bioindicator for blackbirds may provide another important tool for predicting potential impacts to agriculture from high blackbird abundance.

Study Area

Bird Conservation Region 11 (BCR11) occurs in five states and three provinces, and covers over 715,000 km² (Figure 1). Glaciers contributed to the formation of BCR11 12,000 years ago when they melted and left behind depressions that collected rain and snow melt (Leitch 1989). Large fluctuations in hydrologic regimes create diverse vegetation structure in BCR11. During the dry season, locations which are deep enough to have standing water are dominated by submergent vegetation. Vernal potholes primarily support grasses, sedges, and forbs (Kantrud 1989). The ecology of BCR11 has been adversely impacted by widespread agricultural practices (Euliss et al. 1999). Temperature and precipitation conditions combined with fertile soil make the landscape favorable for a wide variety of agriculture. Bird Conservation Region 11 generally has a sparse human population with

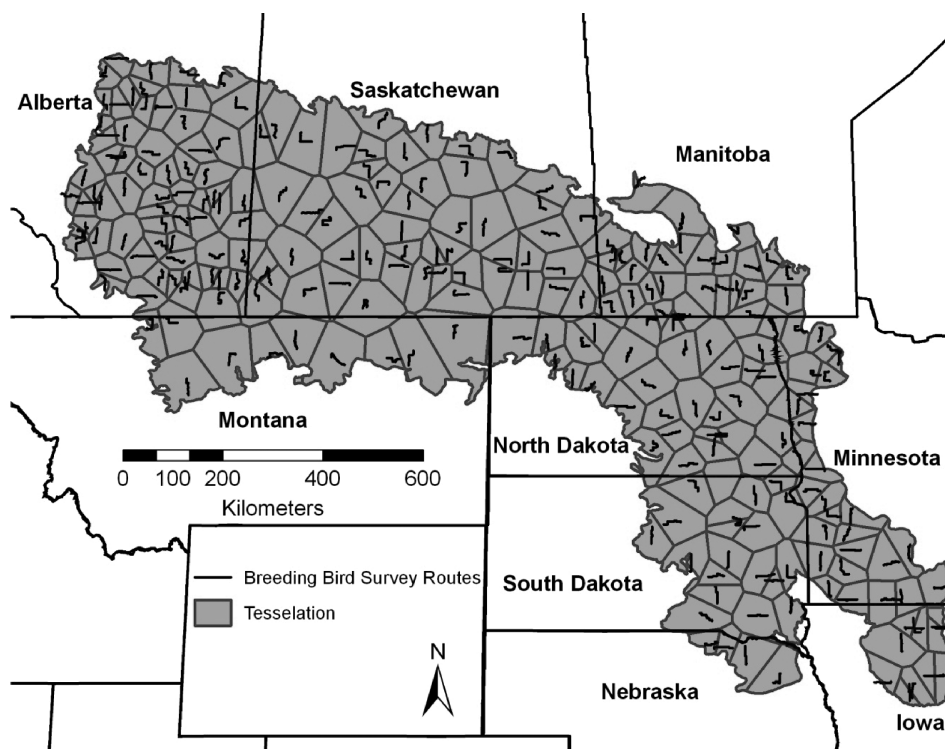


Figure 1. Tessellation and distribution of 245 North American Breeding Bird Survey (NABBS) routes in Bird Conservation Region 11 across the United States and Canada. Data from 1980–2000 was used in these analyses.

farms and larger urban areas increasing in size (Leitch 1989). In addition to agriculture, continued increases in urbanization and a concomitant increase in road construction negatively impact the ecology of BCR11 (Euliss and others 1999). Before European settlement, the region consisted of approximately 10% wetland (Mitsch and Gosselink 2000); however, it is estimated that over half of pre-existing wetlands have been drained for agriculture (Leitch 1989). Remaining wetlands in BCR11 are heavily impacted by agriculture-induced sedimentation, excessive nutrient inputs, and agricultural chemicals (Euliss and others 1999). Extremes in precipitation and temperature are common across BCR11. The region is typically colder and wetter to the north and east, and warmer and drier to the west and south (Kantrud 1989). Temperatures in BCR11 are generally cold with the mean daily temperatures at or below 0°C for 5 months of the year. Air temperatures in the winter can drop below –60°C and can exceed 40°C during the summer (Euliss and others 1999).

Methods

Historical Data Sets

Data for this study were obtained from North American Breeding Bird Survey (NABBS) routes within BCR11 from 1980–2000 (Sauer and others 2005). The NABBS is a long-term survey effort to monitor the status of bird population trends at a continental scale. Breeding bird survey routes are randomly assigned along roadsides across North America,

and surveys are conducted during late May and June. Each route is 39.4 km in length, and there are 50 stops approximately every 0.8 km along the route. A 3-min point count is performed at each stop, and all birds seen or heard within a 402-m radius are recorded. Individual routes are surveyed by the same observer each year, when possible, with a consistent method and only under suitable weather conditions (*i.e.*, low wind and minimal precipitation) where bird detection probabilities are not likely to be affected. This survey protocol attempts to minimize variability in NABBS data to insure that data are as unbiased as possible and that real variation in trends can be detected over time. We used NABBS data between the years 1967–2004 which represent the range of time data that were available at the time of analyses. We used data from 245 routes in BCR11 (Figure 1); data from 193 routes were used to create spatial models, while data from 52 routes were withheld for validation purposes. Breeding bird survey routes surveyed a variety of habitats across the BCR11 including, agricultural, pothole, and prairie habitat.

Modeling Approach

Blackbird abundance was modeled as a function of nuisance effects and waterfowl abundance of various species using a hierarchical modeling approach within a Bayesian framework. Hierarchical models are useful for modeling NABBS data because they acknowledge correlation among multiple observational units which are present in the survey design. Among routes, spatial correlation occurs because routes that are closer together have more similar counts than routes that are further apart. Temporal correlation occurs across time because routes that are surveyed closer together in time have more similar counts than routes that are further apart in time. Observer effects constitute another level in the hierarchical model. Bird surveying experience among observers can substantially bias counts, and failure to accommodate for this effect can substantially affect analyses (Sauer and others 1994). Hierarchical models are best fit using Bayesian approaches because all unknown quantities are treated as random variables (Link and Sauer 2002).

We used Poisson regression to blackbird abundance as a function of waterfowl abundance in BCR11 because counts are typically discrete positive values and are often Poisson distributed. Models were fit using Markov chain Monte Carlo (MCMC) techniques using Gibbs sampling (Link and others 2002). The Gibbs sampling algorithm samples from the posterior distribution of a random variable (Gelman and others 2004). Markov chain Monte Carlo simulations were run for 60,000 iterations, including a 50,000-iteration burn-in period required for convergence. At the beginning of the burn-in period the prior values heavily influence the posterior distribution. During the convergence period in an MCMC simulation, dependence on the prior is lost and the posterior distribution becomes heavily influenced by the data. Spatial models were fit using WinBUGS 1.4.1, which provides a means to run MCMC simulations using Gibbs sampling (Spiegelhalter and others 2003).

We used data from 3,797 NABBS counts surveyed by 446 observers from 1967–2004 to model bird abundance as a function of waterfowl numbers in BCR11. The response variable in the models is the total number of birds across the entire route for each year for each blackbird species. The hierarchical model accounted for nuisance effects at three levels in the hierarchy. A year effect was included to account for temporal variation in bird abundance over time. Two observer effects were included in the model: one accounted for differences in surveying abilities among observers (Sauer and others 1994), and the other effect accounted for inexperience (a first-time observer effect). The first-time observer effect was a binary variable which is “0” if it was an observer’s first time surveying a

route and a “1” if the observer had previously surveyed the route. Observers with little experience are often less familiar with species found on their route and less efficient at completing the survey than more experienced observers (Kendall and others 1996). Because routes that are in closer proximity will have similar habitat characteristics, they will likely have similar bird species composition and abundance which create spatial autocorrelation among routes. Spatial autocorrelation was accounted for by using a spatial conditional autoregressive (CAR) prior distribution on the route effect (Banerjee and others 2004). We used a tessellation to create an irregular lattice around NABBS routes within BCR11 (Hooge and Eichenlaub 1997) (Figure 1); this lattice is used to derive an adjacency matrix of neighboring routes. Spatial autocorrelation is accounted for when routes share a common boundary in the tessellation; distances among routes are not taken into account (Thogmartin and others 2004).

One large difference between Bayesian approaches to model fitting and traditional frequentist techniques is the inclusion of prior information which influences the final outcome. Prior information (henceforth “priors”) can be either specific when previous information is available or vague when pre-existing knowledge is not known. Because little information is known about how blackbird populations are related to waterfowl numbers, vague prior distributions were assigned to parameters in the model (Link and Sauer 2002). During the convergence period the information in the data influence the result and influence from the priors becomes minimal. Breeding bird survey counts are represented by (λ) and occur across space (S) along with other covariates. Year (γ_k), and observer (ω) effects in counts were given mean zero normal distributions; beta parameters (β_k), spatial effects (Z), and novice effects (η) were given normal distributions with a mean of 0 and variance equal to 1000 (Link and Sauer 2002, Thogmartin et al. 2004).

The final model used was:

$$\log[\lambda(s)] = \sum_{k=1}^n \beta_k x_k(s) + Z_k(s) + \omega_k(s) + \eta I(s) + \gamma_k(s)$$

Thogmartin et al. (2004, 2006) used this hierarchical model to examine the influences of environmental covariates on cerulean warblers (*Dendroica cerulea*) and five grassland bird species. An overdispersion effect (ϵ_k) used by Thogmartin and others (2004, 2006) was not included in this model because both red-winged blackbird and yellow-headed blackbird counts show less overdispersion than counts of rare species examined in other studies (Forcey and others 2007).

Blackbirds in BCR11 share wetland habitats with a wide variety of waterfowl. We reviewed published habitat associations and life histories for both blackbirds and waterfowl to determine the waterfowl species that would be most likely associated with blackbirds based on habitat preferences (Table 1). Life history was evaluated for gadwall (LeSchack and others 1997), American wigeon (Mowbray 1999), mallard (*Anas platyrhynchos*) (Drilling and others 2002), blue-winged teal (Rohwer and others 2002), northern shoveler (Dubowy 1996), northern pintail (Austin and Miller 1995) green-winged teal (Johnson 1995), redhead (Woodin and Michot 2002), canvasback (Mowbray 2002), lesser scaup (*Aythya affinis*) (Austin and others 1998), ruddy duck (*Oxyura jamaicensis*) (Brua 2002), red-winged blackbird (Yasukawa and Searcy 1995), and yellow-headed blackbird (Twedt and Crawford 1995). Abundances of these waterfowl species were used as covariates in a global model for each blackbird species. All waterfowl species were included in the global model because none of the species abundances were highly correlated ($r < 0.7$). Slopes of

Table 1

Posterior distributions of waterfowl covariates from the global model for evaluating blackbird and waterfowl abundance relationships.

Means and 95% credibility intervals are presented

Blackbird Species	Waterfowl Species	Mean ^a	95% LCL	95% UCL
Red-winged Blackbird	Gadwall	-0.009	-0.012	-0.006
	American Wigeon	0.006	0.001	0.010
	Mallard	0.024	0.019	0.028
	Blue-winged Teal	0.027	0.023	0.031
	Northern Shoveler	0.028	0.023	0.033
	Northern Pintail	-0.013	-0.018	-0.008
	Green-winged Teal	0.007	0.000	0.013
	Redhead	0.016	0.009	0.023
	Canvasback	0.018	0.014	0.022
	Lesser Scaup	-0.005	-0.009	-0.001
	Ruddy Duck	0.017	0.013	0.022
	Spatial Conditional Autoregressive	0.007	0.003	0.010
Yellow-headed Blackbird	Gadwall	0.017	0.011	0.023
	American Wigeon	-0.039	-0.045	-0.032
	Mallard	0.019	0.013	0.026
	Blue-winged Teal	0.073	0.066	0.079
	Northern Shoveler	-0.028	-0.035	-0.022
	Northern Pintail	0.021	0.015	0.028
	Green-winged Teal	0.104	0.094	0.115
	Redhead	0.033	0.022	0.045
	Canvasback	0.036	0.031	0.041
	Lesser Scaup	-0.007	-0.013	0.000
	Ruddy Duck	0.022	0.013	0.031
	Spatial Conditional Autoregressive	0.011	0.006	0.015

^aMean represents a model averaged value of the beta parameter based on the values of the beta parameters in each model and the corresponding weight (w_i) of each model (Burnham and Anderson 2002).

the beta parameters from the global model revealed the type of relationship (positive or negative) each waterfowl had with each blackbird species and the relative strength of the relationships. Waterfowl numbers were standardized using a Z-score before model fitting to improve MCMC convergence and allow relative comparisons of model slope coefficients to assess the strength of the associations (Gilks and Roberts 1996).

Model Evaluation

Data from 52 NABBS routes in BCR11 were withheld from model construction so known abundance information from these routes could be compared with estimated abundances

generated from the global model. Estimated abundances calculated by WinBUGS from the best model were based on prior information, information in the data, and the value of the beta parameters in the model. Abundance values calculated from withheld routes were compared with known information using simple linear regression. Our models were evaluated using two aspects of model validation: discrimination and calibration. We compared the ability of the model to predict abundance by comparing the slopes of the regression line to a 1:1 correspondence line (calibration) and by examining the R^2 values of the regression line (discrimination). All regression analyses were performed using R (R Development Core Team 2005).

Results

Hierarchical modeling efforts showed that blackbird abundance can be reliably modeled as a function of waterfowl numbers. Although, relationships between blackbirds and individual waterfowl species were weak, few 95% credibility intervals overlapped zero indicating high precision of the estimates. Most waterfowl species were positively associated with blackbird (especially Green-winged Teal and Yellow-headed Blackbird) numbers although negative associations did exist for some waterfowl species (Table 1).

Red-winged blackbirds were most strongly associated with mallards, blue-winged teal, and northern shovelers, and associations with these species were positive; other positive relationships occurred with other waterfowl species but were weaker. Negative relationships occurred with red-winged blackbird and gadwall, northern pintail, and lesser scaup. Yellow-headed blackbirds were most strongly associated with green-winged teal; weaker positive correlations occurred with other species. Negative associations occurred with American wigeon, northern shoveler, and lesser scaup (Table 1).

The discrimination component of our validation showed that hierarchical models predicted blackbird abundance reliably ($R^2 = 0.27$ – 0.41). The model predicting red-winged blackbird abundance had good fit, while the yellow-headed blackbird model had poorer fit (Figure 2). The validation component of our analyses supported this finding with a stronger

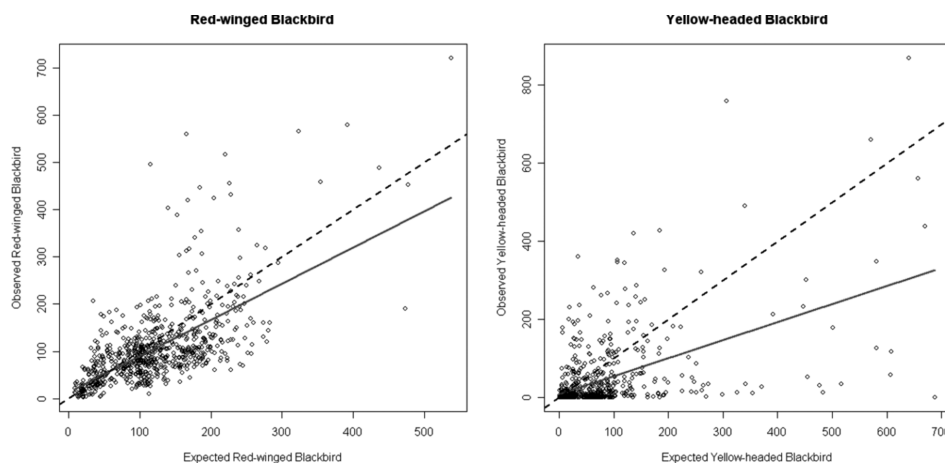


Figure 2. Simple linear regression plots validating spatial models for predicting blackbird abundance using waterfowl species as covariates in Bird Conservation Region 11 ($n = 702$, $P < 0.001$ for each species). The solid line represents the least squares regression line, and the dotted line represents a 1-to-1 correspondence line.

fit to the 1:1 correspondence line for red-winged blackbirds than yellow-headed blackbirds (Figure 2).

Discussion

Relationships between blackbirds and individual waterfowl species were generally weak compared to those of land-use and climate (Forcey 2006, Forcey and others 2007), however a global model provided a good fit for predicting red-winged blackbird abundance. While slope coefficients were small, precision was high which led to few 95% credibility intervals overlapping zero. Spatial structure also was weak for both blackbird species indicating that spatial autocorrelation is not an important effect in these models.

As hypothesized, most blackbird-waterfowl relationships were positively related to one another. This is likely due to similar general habitat characteristics that blackbirds and waterfowl share. While the waterfowl that we examined in this study vary in specific habitat preferences (e.g., some nest in uplands while others prefer emergent vegetation), all use wetland habitat in some way. Despite habitat similarities, some species of waterfowl showed inverse relationships with blackbird numbers. Gadwall numbers were inversely related to red-winged blackbirds which may be attributed to the gadwall's preference for larger wetlands (LeSchack and others 1997) compared to red-winged blackbirds which are generalists and will nest in small wetlands as well as other habitats (Yasukawa and Searcy 1995). American wigeons were inversely related to yellow-headed blackbird abundance which may be explained by American wigeons' preference for shallow wetlands (Mowbray 1999), whereas yellow-headed blackbirds prefer deep-water wetlands (Twedt and Crawford 1995). These habitat preferences also explain the inverse relationship between yellow-headed blackbirds and northern shovelers which prefer shallow wetlands shunned by yellow-headed blackbirds (Dubowy 1996).

While many waterfowl-blackbird relationships can be explained by habitat similarities, there were some waterfowl that showed unexpected negative associations with certain blackbird species. We were unable to explain the negative relationship between red-winged blackbirds and northern pintail numbers. Northern pintails frequent shallow, semi-permanent wetlands with emergent vegetation (Austin and Miller 1995), so it is unclear why this species was not positively associated with red-winged blackbirds which frequent similar habitats. Lesser scaup were negatively associated with both yellow-headed blackbirds and red-winged blackbirds. This finding was also unexpected as lesser scaup frequent wetlands with emergent vegetation (Austin and others 1998), the same general habitat preferred by both red-winged blackbirds and yellow-headed blackbirds. One explanation for the negative association between lesser scaup and yellow-headed blackbirds can be attributed to the lesser scaup's preference to nest in uplands, whereas yellow-headed blackbirds nest in deep-water wetlands. These findings and other unexpected negative associations between blackbirds and certain waterfowl species may be due to factors other than habitat and warrant further study.

Additional sources of bias in our models are derived from inherent biases presented in the NABBS. Our model accommodates three sources of bias present within the NABBS: yearly variation, variations among routes, and bias among observers. Additional sources of bias that we were unable to account for include: roadside bias and detectability differences among species. Roadside bias occurs because all breeding bird surveys occur along roadsides and therefore the habitat may not be representative of habitat far away from roads (Keller and Scallan 1999). While this bias may affect the overall birds observed, the fact this bias is consistently present across all surveys may

minimize its effect on our models. Species detectability issues occur when some species are more conspicuous than others because of habitat preferences or behavioral differences (Palmeirim and Rabaca 1994). For example, red-winged blackbirds may be counted more reliably because they sing conspicuously on cattail vegetation (Yasukawa and Searcy 1995) whereas redhead ducks may be undercounted because they nest inconspicuously in dense cattail vegetation (Woodin and Michot 2002). Ultimately this can lead to some species being more misrepresented in a survey than others. Unfortunately without a species-specific measure of detectability, it is difficult to estimate the degree this bias affects our models.

Results of discrimination and calibration validation showed that a global model of all 11 waterfowl species in my analysis served as reliable predictor variables for red-winged blackbirds ($R^2 = 0.41$) and less reliably for yellow-headed blackbirds ($R^2 = 0.27$). The model generally over-predicted abundance for yellow-headed blackbird. Red-winged blackbirds were predicted reliably at lower observed abundances; at the higher range of observed abundance the model tended to under-predict red-winged blackbird abundance.

Sunflower depredation by blackbirds remains a prominent agricultural issue for farmers in the northern great plains of North America. The importance of the issue places many responsibilities on not only sunflower growers, but also wildlife managers. The ability to use waterfowl numbers as bioindicators of blackbird abundance has important implications for a wildlife manager. Predicting annual relative blackbird numbers through waterfowl as bioindicators could give managers baseline information on the extent that avian depredation will affect sunflower growers. However managers trying to predict blackbird numbers from waterfowl will have to carefully consider abundances from many species to arrive at a reliable prediction. Even then, predictions are only likely to be reliable for red-winged blackbirds as validation plots for yellow-headed blackbirds showed poorer fit. Although models showed good fit for red-winged blackbirds, there are two primary limitations for implementing waterfowl as bioindicators for blackbirds in a management framework. First, the complexity of the model and the amount of data required to obtain meaningful predictions may limit the feasibility of this approach. Second, there is a considerable lag time before waterfowl abundance data are available to use in a modeling framework. Typically a full year elapses before waterfowl abundance data are available for the preceding year. The absence of waterfowl data for the current year would limit how this modeling approach could be used in a management framework to predict blackbird numbers. Despite these limitations, these modeling efforts have provided useful information on blackbird-waterfowl relationships, and this information can be useful from an academic, historical, or bioindicator perspective.

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